

Further Observations on the Natural History of
Philaethria dido dido (Lepidoptera: Nymphalidae: Heliconiinae)

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Abstract: Observations on the life cycle and natural history of *Philaethria dido dido* (Lepidoptera: Nymphalidae: Heliconiinae) as studied in northeastern Costa Rica are summarized. Emphasis is placed on: (1) additional descriptions of life stages, (2) a larval food plant record (*Passiflora vitifolia*-Passifloraceae), (3) developmental time in the laboratory (37-39 days), and (4) various behavior patterns associated with oviposition and larval development. These data and other information from the literature are discussed from the standpoint that *P. dido* is a specialized insect of tropical rain forests and that it has a widespread but strongly localized geographical distribution pattern in Central and South America.

INTRODUCTION

Owing perhaps to their apparently close evolutionary history with the Passifloraceae and their roles in mimicry complexes, neotropical butterflies of the subfamily Heliconiinae have received considerable attention from biologists interested in phylogeny, ecology, and behavior (e.g., Kaye, 1917; Beebe, 1955; Beebe, Crane, and Fleming, 1960; Crane, 1957; Emsley, 1963; 1964; 1965; Benson, 1971; Turner, 1971; Brown and Mielke, 1972). Of the seven genera in the subfamily, the genus *Philaethria* comprises a single conservative subdivision and represents a different lineage of heliconiine evolution from the other two subdivisions (Emsley, 1963). Since *Philaethria* is conservative in the sense of exhibiting many subfamily characteristics in their most generalized form and has very few specializations (Emsley, 1963), studies of member species in this genus are predicted to provide more information on the general ecological and behavioral adaptations of the subfamily as a whole. The paper of Beebe, Crane, and Fleming (1960) gives a detailed account of the early stages and food plants of *Philaethria dido dido* (Clerck) on Trinidad, and Brown and Mielke (1972) provide similar food plant data for both *P. dido dido* and *P. wernickei* (for two subspecies, *wernickei* and *pygmalion*) in extra-Amazonian and Amazonian Brazil. And while *P. dido* has a broad geographical distribution in wet tropical regions of Central and South America (Emsley, 1963;

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Barcant, 1970), a good deal more needs to be learned about the biology of this interesting butterfly throughout this range. At least part of the reason why the butterfly has not been studied in Central America stems from the elusive habits of this insect: Many authors report that it is a high flier, preferring the canopy of virgin forests; it is seldom seen near the ground.

This paper summarizes some further observations on the biology of *P. dido* (Fig. 1) on the Central American mainland, with an emphasis on life cycle and natural history. The descriptions of the early stages, so well presented by Beebe, Crane, and Fleming (1960), are supplemented here with the first illustrations of the egg, third and fourth instars, and pupa. An egg-adult developmental time as measured for one species of *Passiflora* is given for the first time. These and other aspects of natural history comprise a new attempt to study the butterfly in Central America.

METHODS

Studies were initiated on July 1, 1973 when I made my first field record of oviposition in *P. dido* in the thinned-out old secondary forest (Fig. 2) that borders the Rio Tirimbina near La Virgen, Heredia Province, Costa Rica. Oviposition was studied on the gentle slope of forest rising from the river but not including the narrow strip of very disturbed young secondary growth where another wet-forest butterfly, *Parides arcas mylotes*, has been studied (Young, 1973). Much of this gentle slope of old secondary forest will be eliminated within two years in a land-clearing project to raise cattle, and it therefore represents one habitat or part of a larger habitat of *P. dido* that is endangered. This general region of Costa Rica on the Caribbean drainage of the Central Cordillera to the west is a basal belt transitional zone between montane and premontane tropical wet forest, and the elevation is about 225 meters.

The thinned-out condition of the forest where oviposition has been repeatedly observed is the result of farm workers beginning to clear the land with machetes, but this was postponed for two years when I spoke to the owner of this land so that various ecological studies of cicadas and butterflies could be completed. The original understory was considerably more dense than it is now (Fig. 2), but the plant species used for oviposition by *P. dido* has remained intact. Oviposition and general flying behavior of adult *P. dido* were observed in this thinned-out forest by walking slowly through 200 meters of forest, then moving about 15 meters to one side (up the slope) and repeating this; the procedure was repeated four times giving a total of five 200-meter transects, and the census was done on July 1-2, 1973; August 12-13, 1973; September 1, 1973. These censuses were conducted while sampling nested quadrats in the forest for exuviae of a large cicada (*Zammara* sp.) which was very active in the adult stage at this time.

Eggs seen to be oviposited in the field were brought into the laboratory for rearing studies. From eggs collected in this way during July and August, I reared a total of eight individuals to the adult stage, keeping records on each one for: (1) external morphology and coloration, (2) duration (days) of each life stage, including separate instars of larvae, and (3) behavior patterns of larvae. Each individual was reared separately in a small clear plastic bag containing fresh clippings of the food plant; the bag was always kept tightly tied to prevent desiccation of the food. All bags (a total of thirteen) were kept together on a shaded shelf in a second-story apartment (Apartamentos Miami) in San José and cleaned every three or four days for removal of fecal material and excess condensation. In order to observe intraspecific interactions among larvae, I occasionally would place three or four individuals together in a plastic bag containing one or two cuttings of the food plant. My interest here was to observe aggressive encounters, or lack thereof, among larvae. All life stages were photographed at the same time that notes were made on coloration and morphology. The adult specimens obtained from these rearings are preserved in my permanent collection and can be made available to interested workers upon request. Owing to the reputed high local variation in the wing color pattern of adult *P. dido* (e.g., Emsley, 1963), students of intraspecific variation in tropical insects might find such collections useful for systematic studies. Pupal shells have also been preserved from this study.

RESULTS

Life Cycle

Since there exists one excellent text account of the life stages of *P. dido* (Beebe, Crane, and Fleming, 1960), it would be redundant to describe the stages as seen in the present study. Rather, I refer the interested reader to the account of Beebe, Crane, and Fleming, and wish only to supplement those observations with figures of the egg, third instar, fourth instar, and pupa (Fig. 3)—stages described but not pictured in Beebe, Crane, and Fleming. I also present some observations on color differences in the fifth instar between Costa Rica and Trinidad and give specific developmental time data for *P. dido* (not given in Beebe et al., 1960), contrasting this developmental time to the general pattern offered by Beebe et al.

Beebe et al. (1960) report that the head of fifth instar is bright orange, but for the Costa Rican individuals studied the head is clearly beige and slightly shiny. At the base of each of the two head scoli there is an irregularly shaped black spot not given in Beebe et al., and the portions of the body described in Beebe et al. as being white are pale green throughout the fifth instar in the Costa Rican *P. dido* studied. The supralateral thoracic scoli in the Costa Rican fifth instars do not have black tips and the basal portion



FIG. 1. An adult male *Philaethria dido dido* (dorsal view). This is one of the individuals obtained from eggs collected at Finca Tirimbina, La Virgen, Heredia Province, Costa Rica, July 1973.

of each is distinctly orange while the shaft is red. This does not occur in Trinidad *P. dido*. Furthermore, the sublaterals of abdominal segments in Costa Rica are greenish-white with faint black tips, and not the white-orange-black pattern as seen on Trinidad (Beebe et al., 1960). The longest scoli on the Costa Rican fifth instars are 8–9 mm long.

Beebe et al. (1960) also state that the usual duration of the egg stage in Trinidad heliconiines (including *P. dido*) is about four days. For Costa Rican *P. dido* at about 23°C and humid confined bags, the egg stage lasts seven days. The entire larval period is about nineteen days, with the first instar lasting three days, the second three days, the third three days, the fourth about four days, and the fifth about six days.

Beebe et al. (1960) state that pupae of the "group A type," which includes (in addition to *P. dido*) *Agraulis vanillae*, *Dione juno*, *Dryadula phactusa*, *Dryas julia*, and *Heliconius doris*, are generally brown in color. I figure the pupa of *P. dido* here (Fig. 3F) to point out its distinct mottled color pattern as seen in Costa Rica. The pupa is about 30 mm long and resembles a piece of broken-off, rough tree bark, being mottled boldly in various shades of brown and gray. It is perhaps one of the most cryptic of heliconiine pupae.



FIG. 2. The thinned-out old secondary forest habitat at the edge of transitional-zone rain forest at Finca Tirimbina where female *P. dido dido* oviposits on *Passiflora vitifolia* (Passifloraceae) vines that grow along the ground and over rocks and tree stumps.

The pupa for Costa Rican *P. dido* lasts about eleven days for the male and twelve or thirteen days in the female. Beebe et al. do not give a typical duration figure for the pupal stage.

From these considerations, the overall egg-adult developmental time for *P. dido* in laboratory culture in Costa Rica is 37 to 39 days. Some discrepancies between the present study of *P. dido* and the larval developmental time generalizations of Beebe et al. (1960) for heliconiines include: (1) the first and second instars of three days as opposed to two days, (2) the fourth instar of four days, and (3) the usual duration of the fifth instar of six days instead of the usual five days. The overall larval period noted by Beebe et al. is twelve days as opposed to the nineteen days found here for *P. dido*.

Larval Food Plant

The plant used for oviposition is *Passiflora vitifolia* and it occurs at the study site as a large, sprawling vine on the ground, logs, and tree stumps. The vine does not go into the canopy here, but it is difficult to say if this has

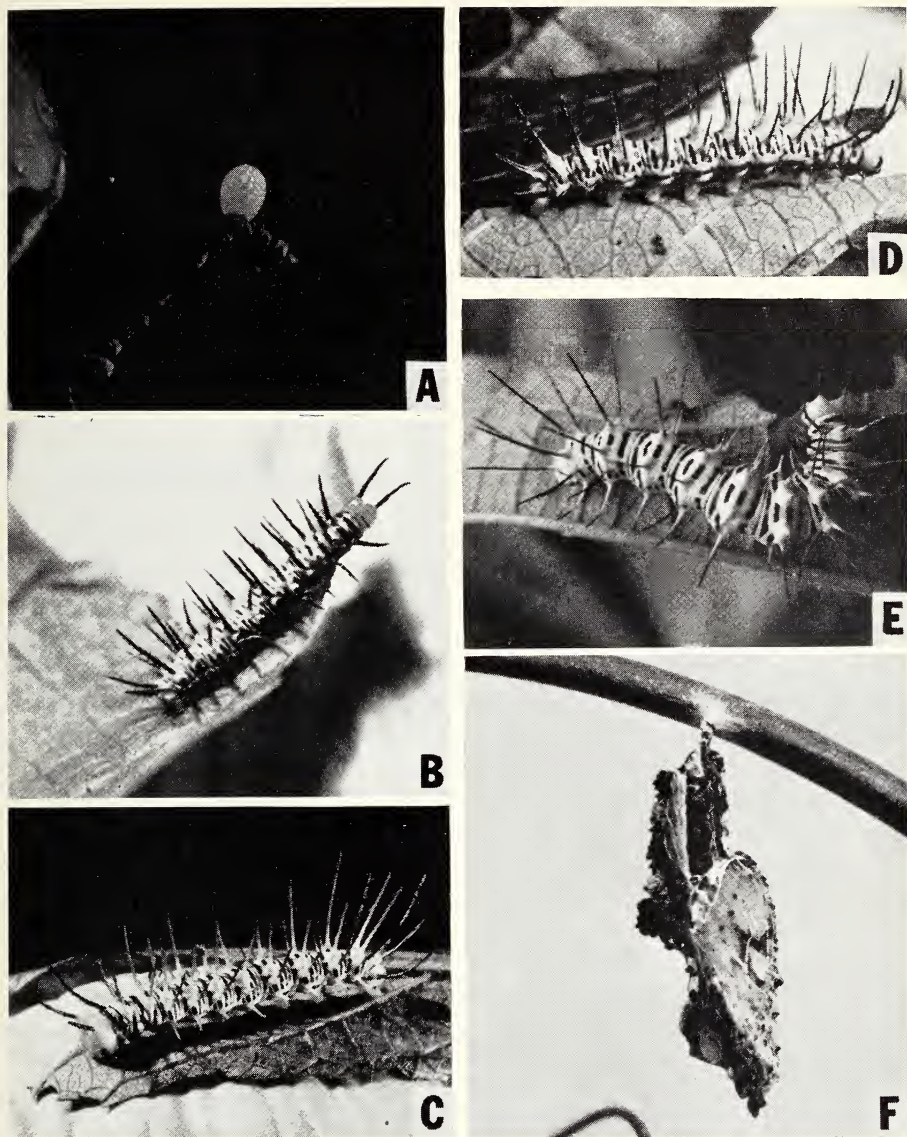


FIG. 3. Some life stages of *P. dido dido* in Costa Rica. (A) egg, (B) third instar larva, (C) fourth instar larva showing one aspect of scoli distribution and coloration, (D) fourth instar larva showing another aspect of scoli distribution and coloration, (E) fifth instar, dorsal view, and (F) the pupa, lateral view.

always been the case owing to the selective thinning out of trees by farmers. But the large size of the sprawling vine near the ground is indicative of successful thriving in this zone of the forest environment. The leaves are thick and with rough texture. I have not found other heliconiines on this species of *Passiflora* in the study site, but at Rincon de Osa, a lowland tropical wet-forest site on the southern Pacific coast of Costa Rica, Dr. Woodruff W. Benson (pers. comm.) has found *P. dido* and several other heliconiines feeding on this plant. It is a species of *Passiflora* that has clearly been exploited by heliconiines at different stages in the evolutionary development of the subfamily. It appears to be a favorite food plant for the subfamily at wetter lowland sites in Costa Rica and other regions of southern Central America.

The larvae of all instars for *P. dido* feed primarily on the older and larger leaves of *P. vitifolia* as studied in the laboratory. But this may also be true in the wild since eggs are laid on older leaves (see below).

Oviposition Behavior

Some authors (e.g., Barcant, 1970; Brown and Mielke, 1972) have commented that *P. dido* is a high flier over treetops in forests. But oviposition clearly sometimes occurs near the ground as seen in the present study. For all of the times I observed oviposition, it occurred in sunny weather, either in the morning or early afternoon. The typical flight pattern of female *P. dido* would be to appear suddenly in the lower portion of the thinned-out forest and make several attempted ovipositions before actually laying an egg. In several instances, the female would actually grasp a tendril or leaf with wings fluttering for stability, but an egg was not laid. I followed one female on July 2 and it was almost twelve minutes before an egg was laid, despite several intervening attempts at oviposition. The pattern is somewhat frustrating to the observer since it almost appears as if the *Passiflora* species in question was not acceptable to *P. dido*.

The bright yellow large egg is laid either on the ventral side of an older leaf of *P. vitifolia*, or else on a dead tendril. In a total of fourteen eggs actually observed to be oviposited, nine were on leaves and the remaining five on dead tendrils. The female flies very erratically between ovipositions or attempted ovipositions, suddenly darting up into the canopy and then coming back down to the *Passiflora*. A single female will remain in the same general area where the *Passiflora* is growing for as long as 25 minutes in my experience. Out of a total of probably five different females of *P. dido* observed ovipositing during July and August, three of these were very fresh individuals, and could not have been more than a day or two out of the chrysalis. It is especially easy to distinguish very young or fresh adults in *P. dido* since, as noted by Emsley (1963), wing color fades very rapidly in this species. Females of *P. dido* may therefore be mated almost immediately after emerging

from their pupae. It is not known, however, if males wait near female pupae for future mates, as noted for *Ornithoptera* (Papilionidae) species (Borch and Schmid, 1973).

Larval Behavior

The first instar larva devours its empty eggshell, and during subsequent molts, larvae also eat their castoff exuviae. These two behavior patterns have not been previously reported for *P. dido* by Alexander (1961a). In terms of feeding on leaf tissue, the larvae exhibit the channeling behavior reported by Alexander (1961a) for *Dione*. The larvae of *P. dido* do not remove fecal material with the jaws as described in Alexander (1961a) for the larvae of several *Heliconius*. The resting behavior, not studied for *P. dido* by Alexander, is very variable in the laboratory, but usually involves the larva facing the direction of feeding; often a larva assumes a hooked or "J" position as noted by Alexander for *Heliconius isabella*, *H. melpomene*, and *H. ricini*.

Weaving is also well expressed in the construction of silken pathways along stems and ventral sides of leaves. Disturbed larvae are very mobile for several minutes, and they walk very fast. As in *Heliconius erato* (Alexander, 1961a), the larvae of *P. dido* are clearly asocial and very aggressive and there are no signs of any gregarious behavior (including social defecation) of the type so evident in *Dione juno* (Alexander, 1961a; Muysshondt, Young, and Muysshondt, 1973). Individual larvae do not share the same leaf without fighting, as seen in laboratory culture. Another aspect suggesting that *P. dido* is truly a solitary species is the complete lack of synchrony among larvae for feeding and resting. From these observations, I suspect that the larvae of *P. dido* are considerably more aggressive and asocial than originally predicted by Alexander, thus being closer to the behavior patterns of *H. erato* than to *H. melpomene* or *Dione*.

DISCUSSION

The above observations are intended to supplement what has been already determined of the life cycle and natural history of *P. dido* as studied in Trinidad (Beebe, Crane, and Fleming, 1960; Alexander, 1961a; Emsley, 1963; Barcant, 1970) and Brazil (Brown and Mielke, 1972). This report concerns the butterfly in Central America where I am sure several researchers have reared the species in the past.

One of the interesting characteristics of the distributional biology of *P. dido* is the apparently widespread but strongly localized occurrence of the butterfly in the rain forests of Central and South America. The species is susceptible to regional restriction by land barriers: Brown and Mielke (1972) comment that in extra-Amazonian Brazil this species and several other heliconiines are restricted to tropical regions by high southeastern coastal mountains but that it and *P. wernickei* are sympatric over the lower and middle Amazon

Basin and along the eastern coast of Brazil (as far south as Rio de Janeiro). In Costa Rica, the distributional pattern is also molded by the Central Cordillera and confines the butterfly to all of the Caribbean lowlands and southwestern Pacific wet lowlands. The butterfly seldom occurs above 400-meters elevation in Costa Rica, although an occasional adult is seen at elevations as high as 900 meters. The butterfly is also rare in lowland Guanacaste Province, where there is a strong but variable dry season each year.

Various authors (Emsley, 1963; Barcant, 1970; Brown and Mielke, 1972) have emphasized that *P. dido* inhabits forest clearings and edges of rain forests. The same pattern is seen in Costa Rica, although studies are lacking from the canopy in the interior of forests. Certainly one larval food plant, *P. vitifolia*, is abundant in thinned-out forest at their edges; the distributional pattern of such plants and the spectrum of *Passiflora* species exploitation by *P. dido* are the major determinants of habitat selection for oviposition and larval development.

The literature suggests that there may exist considerable specificity for certain species of *Passiflora* in *P. dido*. Beebe, Crane, and Fleming (1960) noted that although the usual food plant in Trinidad is *P. laurifolia*, oviposition (I am equating oviposition with correct larval food plant) also occasionally occurs on *P. cyanea*. Brown and Mielke (1972) report that the preferred food plant is *P. mucronata* in extra-Amazonian Brazil and that larvae refuse *P. alata* and *P. speciosa*, even though both of these are very closely related to *P. vitifolia*, the food plant in Costa Rica (this paper and Woodruff Benson, pers. comm.), and also in Colombia and Panama (Brown and Mielke). Of other Brazilian *Passifloraceae*, *P. dido* also refuses *P. violacea*, *P. jileki*, and *Tetrastylis ovalis* (Brown and Mielke, 1972). Such food plant specialization in *P. dido* in Brazil could have resulted from an evolutionary divergence in food plant exploitation brought about by sympatry with *P. wernickei*, which has been observed (Brown and Mielke, 1972) to feed on other species of *Passiflora* not used by *P. dido*. But clearly other heliconiines might also have exerted some ecological pressure for food plant specialization. However, this is apparently not the case in Costa Rica where several heliconiines exploit *P. vitifolia* at least on the Osa Peninsula. Another important factor to consider is the relative ease with which some species of *Passiflora* can be exploited as larval food plants over others. For example, *Heliconius hecale* and *Agraulis vanillae* are at least two other heliconiines found together on *P. vitifolia* in Guanacaste, Costa Rica (Allen M. Young, pers. obs.). And it is known that *H. hecale* exploits this species over much of Central America and Colombia and as far as Ecuador, along with many other heliconiine species (Keith S. Brown, Jr., pers. comm.). The abundance of this vine and the size of individuals may provide a nonlimited food source for many heliconiines, especially if many of these butterflies have low average fecundities per female (e.g., see Labine,

1968, for *Heliconius erato* egg production). Furthermore, if the local complex of heliconiines exploiting one or a few species of Passifloraceae contains some genera with high dispersal tendencies in the adult stage (see Benson, 1971, for comments concerning generic patterns of heliconiine dispersal tendencies), then this would also lessen the local exploitation of single patches of the vines, a consideration especially important if a given local species of *Passiflora* is very dispersed itself. Although I have not found many other heliconiines on *P. vitifolia* at Tirimbina, this is because systematic searches have not yet been conducted, although I suspect that the herbivore load would be reasonably similar to that observed by Benson on the Osa Peninsula (to be reported by him in a forthcoming paper).

The traditional question of palatability that shrouds ecological and evolutionary approaches to the Heliconiinae is interesting to consider for *Philaethria* butterflies, owing to the generalized separate lineage from other members of the subfamily (Emsley, 1963). If it is assumed that the genetic and physiological adaptations for withstanding toxic compounds derived from plant tissue are a derivative or advanced evolutionary trait in butterflies (Brower and Brower, 1964), the question then arises whether a generalized genus like *Philaethria* has the ability to develop unpalatability. Certainly, the rather convincing resemblance between this butterfly and the presumably palatable mimic *Victorina (Metamorpho) stelenes* (Nymphalidae: Nymphalinae) suggests that *P. dido* is a Batesian model in this interaction (Brower and Brower, 1964), although (1) *P. dido* is absent in El Salvadore where *V. stelenes* is very abundant, and (2) local abundance of *V. stelenes* exceeds that of *P. dido* in young secondary fields in northeastern Costa Rica (Young, 1972). The ability of several of the more primitive heliconiine genera, such as *Agraulis* to feed on *P. vitifolia* suggests that *Philaethria dido* may be palatable, if primitive or generalized genera are unable to develop detoxication systems, as suggested recently by Benson (1971). But since *Philaethria* represents a separate lineage of heliconiine evolution from these other genera, a physiological divergence might have occurred with respect to detoxication systems: *Philaethria* may have evolved them while the clustered lineage of *Agraulis*, *Dione*, *Dryadula*, and *Podotricha* (Emsley, 1963) might not have achieved this, allowing toxic materials to pass out of the gut in fecal pellets. It is clear that the question of palatability, or lack thereof, is still very open in *Philaethria* and warrants further study.

Beebe, Crane, and Fleming (1960) have gone into considerable detail on the comparative analysis of life stages among many heliconiines, including *P. dido*. But I do wish to point out some variations in coloration seen in the fifth instar larva and adult from Costa Rica. It is difficult at the present to attach significance to color differences in the fifth instar between Costa Rica and Trinidad since presumably the same subspecies (*dido*) applies to both regions.

But in the adult series from Tirimbina, the marginal row of light green spots on the dorsal side of each hindwing (Fig. 1) is considerably smaller than in the adult figured in Beebe, Crane, and Fleming (1960). The difference is very stable in all reared adults, and it is also consistent with wild-caught specimens from Tirimbina and nearby Finca La Selva (8 km) that I have obtained over the past five years. Color differences in immatures are difficult to evaluate since they may reflect contemporary ecological specializations and have little or nothing to do with evolutionary history. Brown (1972) comments that the color pattern of older larvae for *Heliconius hermatheria* converges on that of *P. dido* and he interprets this as ecological specialization.

Borrowing from the recent discussion of Benson (1971), it is interesting to cast life cycle and natural historical data for *P. dido* in terms of a pattern of ecological adaptation. Single oviposition, highly aggressive larvae, and apparent food plant specialization are ethological and ecological mechanisms that reflect increased dispersal tendencies of the adult population. From selection pressures favoring a noncohesive adult population, it is also predicted that the opportunity for communal roosting to evolve in *P. dido* would also be very low. In my experience and surely in that of other researchers, *P. dido* adults occur at very low densities in tropical forests, even though a given population might be strongly localized in a region (Brown and Mielke, 1972, point out the latter). I believe that the natural historical observations discussed here and in previous papers are consistent with a non-home-ranging and non-viscous (Benson, 1971) adult population structure for *P. dido* at edges and clearings of tropical rain forests in Central and South America. Localizations of populations of *P. dido* are predicted to be determined primarily by local topographic effects and by a variety of other natural and perhaps man-made land barriers. If topographic barriers are few in a region or become modified by man, we might expect zones of overlap where two or more different forms might co-occur. This would account for the confusion in the literature concerning sympatric populations of *P. dido dido* and *P. dido wernickei* or other varieties on the Central American mainland, while other populations contain only one form, as discussed in Emsley (1963). Especially near breaks in mountains and low hills, we might expect considerable local variety in color pattern, but along the more distal coastal regions, uniformity of the sort encountered in Costa Rica at Tirimbina and La Selva would be expected.

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